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Quantitative and qualitative evaluation of selected wheat varieties released since 1903 to increasing atmospheric carbon dioxide: can yield sensitivity to carbon dioxide be a factor in wheat performance?

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Abstract

The sensitivity of yield and quality parameters to carbon dioxide concentration [CO_2] was determined for individual lines of hard-red spring wheat released in 1903, 1921, 1965 and 1996. All cultivars were evaluated with respect to growth and vegetative characteristics, grain yield and nutritional quality in response to [CO_2] increases that corresponded roughly to the CO_2 concentrations at the beginning of the 20th century, the current [CO_2], and the future projected [CO_2] for the end of the 21st century, respectively. Leaf area ratio ($cm^2\,g^{-1}$) declined and net assimilation rate ($g\,m^2\,day^{-1}$) increased in response to increasing [CO_2] for all cultivars during early vegetative growth. By maturity, vegetative growth of all cultivars significantly increased with the increase in [CO_2]. Seed yield increased significantly as [CO_2] increased, with yield sensitivity to rising [CO_2] inversely proportional to the year of cultivar release. Greater [CO_2] yield sensitivity in older cultivars was associated with whole-plant characteristics such as increased tillering and panicle formation. Grain and flour protein, however, declined significantly with increasing [CO_2] and with year of release for all cultivars, although absolute values were higher for the older cultivars. Overall, these data indicate that yield response at the whole-plant level to recent and projected increases in [CO_2] has declined with the release of newer cultivars, as has protein content of grain and flour. However, if agronomic practice can be adapted to maximize individual plant performance, [CO_2] responsive characteristics of older cultivars could, potentially, be incorporated as factors in future wheat selection.

Keywords: breeding, carbon dioxide, Chris, grain quality, Marquis, Oxen, protein, seed yield, Thatcher, wheat

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Introduction

Data from the carbon dioxide information analysis center indicate a $\sim$30% increase in the global background concentration of atmospheric carbon dioxide [CO_2], from 290 to 375 $\mu mol\,mol^{-1}$ during the last 100 years, with the largest increase in recent decades (i.e. 310–375 $\mu mol\,mol^{-1}$ since 1955, Keeling & Whorf, 2001). It is anticipated that the global background [CO_2] will continue to increase with concentrations projected to approach 500–700 $\mu mol\,mol^{-1}$ by the end of the current century (Intergovernmental Panel on Climate Change scenario's IS 92e and IS 92a, respectively, in Schimel *et al*., 1996). Because rising atmospheric CO_2 represents a resource for plant growth, exploitation of this resource to optimize yield for agronomic productivity has been suggested with future CO_2 increases, and significant intraspecific variation in yield response with a doubling of current CO_2 levels has been observed in cowpea (Ahmed *et al*., 1993), rice (Ziska *et al*., 1996; Moya *et al*., 1998), and soybean (Ziska *et al*., 1998).

The importance of wheat as a global staple for human and animal nutrition is indisputable (e.g. Evans, 1998). Wheat has been grown in the North American prairie for over a 100 years and breeding efforts regarding

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diseases, pest resistance, early maturity, and enhanced grain and baking quality during this time have been continuous (Bonjean & Angus, 2001). The growth and yield response of modern wheat lines has been evaluated with respect to recent 20th century [CO_2] increases (Polley *et al*., 1993), and both old and modern Spring wheat lines have been evaluated for projected, future atmospheric [CO_2] (Mandersheid & Weigel, 1997; Kimball *et al*., 2001). However, wheat lines released throughout the 20th century have not been evaluated regarding the increase in atmospheric [CO_2] that occurred during this period (ca. 30%). Yet, a quantitative and qualitative assessment of reproductive sensitivity to rising [CO_2] for lines released at the beginning and end of the 20th century would be crucial in determining potential changes in yield and quality for both old and modern wheat lines, as well as in identifying those plant characteristics that contribute to [CO_2] responsiveness.

To initiate such an assessment, we evaluated four different lines of spring wheat introduced over the last 93 years, to recent (i.e. 290–375 $\mu mol\,mol^{-1}$) and future increases (i.e. 375–720 $\mu mol\,mol^{-1}$) in atmospheric carbon dioxide at the single plant level. While assessment on a plant basis does not reflect field values, such an approach has distinct validity since increasing yields are related, in large part, to selection for whole-plant characteristics such as harvest index or average kernel weight (e.g. Evans, 1998; Bonjean & Angus, 2001). In the current study, lines were evaluated with respect to the [CO_2] responsiveness of these growth characteristics, as well as vegetative parameters and seed yield. In addition, because increasing [CO_2] can significantly alter protein concentration relative to carbohydrate (e.g. Blumenthal *et al*., 1996; Rogers *et al*., 1998; Kimball *et al*., 2001), wheat and flour quality was determined separately as a function of cultivar and rising [CO_2].

Materials and methods

Because no system has yet been devised to expose plants to subambient [CO_2] under field conditions for 24 h day^{-1} (see Mayeux *et al*., 1993) these experiments were conducted in controlled environment chambers. Seed from four cultivars of hard-red spring wheat (*Triticum aestivum* L.) introduced during the 20th century, Marquis (1903), Thatcher (1921), Chris (1965) and Oxen (1996) were grown using three controlled environmental chambers (EGC Corp., Chagrin Falls, OH, USA) with each chamber maintained at one of three CO_2 concentration set-points, 290, 370 and 720 $\mu mol\,mol^{-1}$ for 24 h day^{-1}. These concentrations approximated the [CO_2] present at the beginning and end of the 20th century as well as that projected for the end of the 21st century. Actual [CO_2] values ($\pm$ SD) averaged throughout the experiment were 293 ± 19, 385 ± 15 and $715 \pm 14\,\mu mol\,mol^{-1}$. Two to three seeds of each cultivar were sown in 0.6 L pots filled with vermiculite and thinned to one seedling 4–6 days after emergence for each [CO_2], 35–40 plants of a given cultivar were used. All pots were watered to the drip point daily with a complete nutrient solution containing 14.5 $mmol\,m^{-3}$ nitrogen (Robinson, 1984). All seed was provided by Dr Ravindra Dezkota of South Dakota State University.

For each chamber, temperature was varied in a diurnal fashion from an overnight low of 20 °C to a maximum afternoon value of 30 °C, with an average daily (24 h) value of 23.1 °C. Average daily temperatures for South Dakota (where Spring wheat is grown exclusively) range from 20 °C in late June during heading, to 24 °C during maturation in July and August, although monthly values as low as 17.5 and as high as 26.5 °C have been recorded (http://www.lwf.ncdc.noaa.gov). Light (photosynthetically active radiation, PAR) was also altered diurnally in conjunction with temperature with the highest PAR value ($\sim$1000 $\mu mol\,m^2\,s^{-1}$) occurring during the afternoon. Daily PAR was 13 h, supplied by a mixture of high-pressure sodium and metal halide lamps and averaged 24.5 $mol\,m^2\,day^{-1}$ for all chambers. The CO_2 concentration of the air was controlled by adding either CO_2 or CO_2-free air to maintain the desired CO_2 concentration. CO_2-free air was obtained using a CO_2 scrubber (Ballston 75–60 type, Ballston Filter products, Lexington, MA, USA). Injection of CO_2 and CO_2-free air was controlled by a TC-2 controller using input from an absolute infrared gas analyzer (WMA-2, PP Systems, Haverhill, MA, USA). Temperature, humidity and [CO_2] were recorded every 15 min and averages recorded on a daily basis for all experimental runs. Additional details concerning the operating system can be found in Ziska *et al*. (2001).

Cultivars were harvested at four different growth stages during development; tiller initiation, flag leaf development, panicle emergence and maturity. These correspond approximately to 2.0, 8, 10.1 and 11.4 on the Feekes small grains scale, respectively. Although the more recently introduced cultivars, Chris and Oxen matured earlier, [CO_2] did not affect the time to maturity for any cultivar. To minimize root binding, all cultivars were transplanted to 4.5 L pots following tiller initiation. Plants from a given cultivar were grouped together, but groups were spaced so as to minimize mutual shading. Both individual plants and groups were rotated weekly inside the chambers until heading to minimize border effects.

At each harvest, eight plants per cultivar and [CO_2] treatment were sampled. Leaf area was determined photometrically on all leaves for the first three growth stages, and estimated from the relationship between leaf weight and area (r^2 of 0.89) from leaf samples for all cultivar–treatment combinations at plant maturity. In addition to leaf area, dry mass was determined separately for leaves, stems and roots at each harvest for all cultivars and [CO_2] treatments following drying at 65 °C for a minimum of 48 h or until dry mass was constant. Root recovery fraction was estimated at approximately 89%. Relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were calculated based on the first two vegetative harvests according to Jones (1985).

Assessment of maturity was based on kernel hardness and leaf senescence. At maturity, plant tiller number was quantified and above-ground biomass determined as described above. In addition, panicles were threshed, seeds were collected and weighed. Seed was bulked among plants for each run and sent to the Western Wheat Quality Laboratory, USDA-ARS, Pullman, WA, USA, for quality analyses. When received, all samples were frozen at −20 °C for 2 days to prevent insect infestation, then cleaned on a Carter dockage tester (Simon-Carter CO., Minneapolis, MN, USA). Test weight was then determined (Method 55-10; AACC, 2000) and seed scoured in a Forester and Son Cyclone Grain Scourer (Model 6, Forster and Son, Ada, OK, USA). Moisture content of grain and flour were determined according to Method 44-16 (AACC, 2000). A ground subsample was used for near infrared reflectance spectroscopy to determine grain hardness (Method 39-70 A; AACC, 2000) using a IA450 near infrared reflectance spectrometer (Technicon, Hoganas, Sweden), and grain protein (Dumas combustion method) (Method 46-30; AACC, 2000) using a model FP-428 (Leco, St Joseph, MI, USA). Grain and flour protein are reported at 12% and 14% moisture, respectively. Traits of single kernels (hardness, weight and size) were assessed using a 300 kernel sample with a single-kernel characterization system (model 4100, Perten Instruments, Springfield, IL, USA). Assessment of flour and protein production was determined by multiplying percentages by grain yield for each experimental run.

Grain was modified to 14.5% moisture content overnight prior to milling. Milling was accomplished using a tempered Quadrument (Brabender) system (Jeffers & Rubenthaler, 1979). Break flour is obtained from the break rollers early in milling and reflects the ease of grain milling (higher values are preferable), while straight-grade flour is the total amount of flour obtained. For quality analysis both straight grade and break flour are expressed as a percent of the total product. Flour ash was determined by Method 08-01 (AACC, 2000) (low values are desired). Milling score is a composite number that encompasses straight flour yield, break flour yield and ash (high values desired). A mixograph analysis reflects mixing time requirement which in turn, is a reliable predictor of loaf volume potential and protein quality (long mixing times are associated with food loaf volumes, Finney et al., 1987). Both ash and mixograph absorption are given at 14% moisture.

Baking of small bread loaves from flour obtained from a given [CO_2] treatment was accomplished using a straight-dough 100 g flour system at optimum water absorption and mixing time following 90 min of fermentation (Method 10-10B, AACC, 2000). Optimum water absorption and mixing time were evaluated by an experienced baker with internal crumb grain score assigned a value of 1 (best) to 10 (unacceptable) by a three member panel of judges. Absorption was calculated on a 14% flour moisture.

Because only three chambers were available, a randomized complete block design was utilized with runs over time as replications (blocks). Each chamber was assigned one of the three CO_2 treatments. At the end of a given run, CO_2 treatments were randomly assigned to a given chamber and the entire experiment was repeated. The entire experiment was repeated four times, and the mean value from each run used as a single replicate. Growth characteristics, vegetative parameters, yield and quality were determined using a two-way analysis of variance with [CO_2] and cultivar as the classification variables (Statview, Cary, NC, USA). Treatment comparisons were made using a Fisher protected least significant difference. Unless otherwise mentioned, significant differences for any measured parameter were determined as being significant at the $P \leq 0.05$ level.

Results

Total plant biomass for the first three harvests indicated a significant effect of both recent and projected increases in atmospheric [CO_2] for all cultivars (Fig. 1). The relative stimulation with each change in CO_2 concentration (i.e. 293–385 and 385–715 μmol mol^{-1}) was approximately the same (ca. 45%) when averaged over all cultivars. However, when divided between 'old' and 'new' cultivars (Marquis and Thatcher vs. Chris and Oxen), the overall relative stimulation of biomass was significantly greater from 293 to 715 μmol mol^{-1} [CO_2] for the older cultivars (52% vs. 39%).

Carbon dioxide had a significant effect on all vegetative characteristics among cultivars, including leaf, stem and average tiller weight as well as tiller

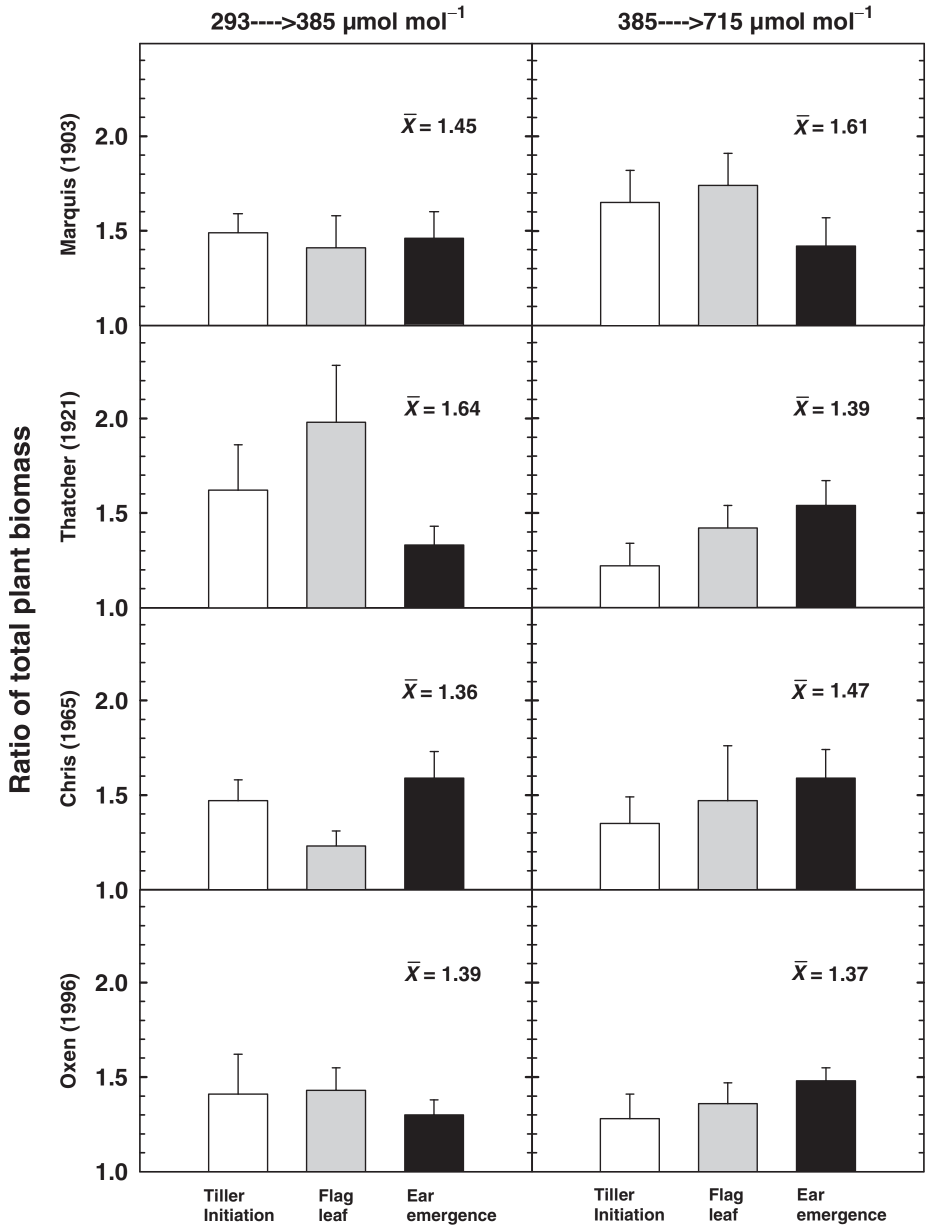

Fig. 1 The ratio of total plant biomass at either 385 : 293 µmol mol^{-1} [CO_2] or at 715 : 385 µmol mol^{-1} [CO_2], for different Spring wheat cultivars released during the 20th century (Marquis, 1903; Thatcher, 1921; Chris, 1965; Oxen, 1996). Biomass ratios were determined at three different periods during vegetative growth: tiller initiation, flag leaf development and ear emergence (these sampling periods correspond roughly to stages 2.0, 8.0 and 10.1 on the Feekes small grain scale). Bars are + SE. All ratios were significantly greater than unity.

number (Table 1). Cultivar variation was significant for all characteristics except leaf area and specific leaf area; whereas significant cultivar by [CO_2] interaction was observed for leaf and stem weight, tiller number, average tiller weight and vegetative biomass (Table 1). Quantification of growth parameters during early vegetative growth indicated an increase in NAR with increasing [CO_2], and a decrease in LAR, with no significant cultivar interaction for either parameter (Table 2). With the exception of Thatcher, no effect of [CO_2] on RGR was observed. Since overall biomass was stimulated by increasing [CO_2], this indicates that carbon dioxide induced changes in RGR must have occurred prior to tiller initiation (i.e. first sampling period).

Seed yield increased significantly for all cultivars with recent and projected increases in atmospheric [CO_2] (Fig. 2, Table 3). Although cultivars responded to

Table 1 Averages and statistical *P*-values of the two-way analysis of variance for cultivars and CO_2 concentration on vegetative characteristics at maturity for four cultivars (cv.) of Spring wheat released during the 20th century (MA, Marquis (1903); TH, Thatcher (1921); CH, Chris (1965); OX, Oxen (1996)) and grown at recent, current and future CO_2 concentrations (293, 385 and 715 μmol mol^{-1})

	Averages							*P*-values		
Variables	293	385	715	MA	TH	CH	OX	Cv. effect	$[CO_2]$ effect	Cv. × $[CO_2]$
Leaf area (m^2)	0.38	0.46	0.57	0.77	0.78	0.20	0.13	–	***	–
Leaf weight (g)	14.4	16.4	20.7	26.7	29.2	8.0	4.9	***	***	**
SLA (m^2 kg^{-1})	23.0	23.6	20.9	23.3	22.9	21.1	22.9	–	*	–
Tiller weight (g)	18.6	24.9	38.1	38.4	40.8	18.1	11.1	***	***	**
Tiller number	42.7	49.2	67.2	77.3	68.0	37.8	33.6	***	***	*
Average tiller weight (g)	0.42	0.49	0.55	0.48	0.59	0.54	0.34	***	***	*
Leaf area per tiller (cm^2)	71.3	74.2	57.3	82.5	99.9	51.2	35.7	***	**	–
Vegetative biomass (g)	61.9	77.7	110.1	111.3	112.3	55.6	43.9	***	***	**

Unless otherwise specified, values are per plant. SLA, specific leaf area.
*$P<0.05$; **$P<0.01$; ***$P<0.001$.

Table 2 Changes in growth parameters, relative growth rate (RGR, g g^{-1} day^{-1}), leaf area ratio (LAR, cm^2 g^{-1}) and net assimilation rate (NAR, g m^2 ay^{-1}) determined from the first two vegetative harvests for Spring wheat grown at 293, 385 and 715 μmol mol^{-1} carbon dioxide (CO_2)

Cultivar	Year of release	$[CO_2]$	NAR	LAR	RGR
Marquis	1903	293	12.7b	121.5a	0.154
		385	14.3ab	104.4b	0.149
		715	15.4a	97.4b	0.150
Thatcher	1921	293	12.7b	109.7a	0.139b
		385	14.0b	109.0a	0.153ab
		715	17.3a	93.6b	0.162a
Chris	1965	293	14.1b	105.6a	0.149
		385	14.3b	96.5ab	0.138
		715	16.7a	89.3b	0.149
Oxen	1996	293	14.7b	100.9a	0.148
		385	16.9b	91.3b	0.154
		715	20.8a	77.1c	0.160

These levels correspond to CO_2 concentrations that approximate the beginning of the 20th century, current and projected atmospheric levels, respectively. Different letters for a given cultivar and column indicate significant $[CO_2]$ treatment differences (Fisher protected LSD).

increasing $[CO_2]$, the relative response decreased relative to the year in which the cultivar was introduced, as indicated by both slope and r^2 values (Fig. 2). This resulted in a significant $[CO_2]$ by cultivar interaction, which was also observed for a number of mature panicles, the percentage of tillers with panicles, and average panicle weight (Table 3). Individual effects of cultivar and $[CO_2]$ treatments were significant for all reproductive characteristics (Table 3).

To determine the basis for cultivar by $[CO_2]$ variation in seed yield, vegetative parameters were compared with seed yield response. Two of the vegetative parameters showing the strongest correlation with seed yield were tillers per plant and leaf area per tiller. Although r values are positive for both old and new cultivars, the plasticity of new tiller formation in response to increasing $[CO_2]$ was greater for Marquis and Thatcher than for Oxen or Chris (Fig. 3a, b). Similarly, the response of leaf area per tiller to increasing $[CO_2]$ was larger for the older cultivars (Fig. 3c, d).

Three key indices of grain quality, percent protein in flour, grams of protein per plant, and grams of flour per plant, were significantly affected by increasing $[CO_2]$ and/or cultivar (Fig. 4). Percentage protein declined both as a function of increasing $[CO_2]$ and with later cultivar releases, although no significant cultivar by $[CO_2]$ interaction was observed. However, significant

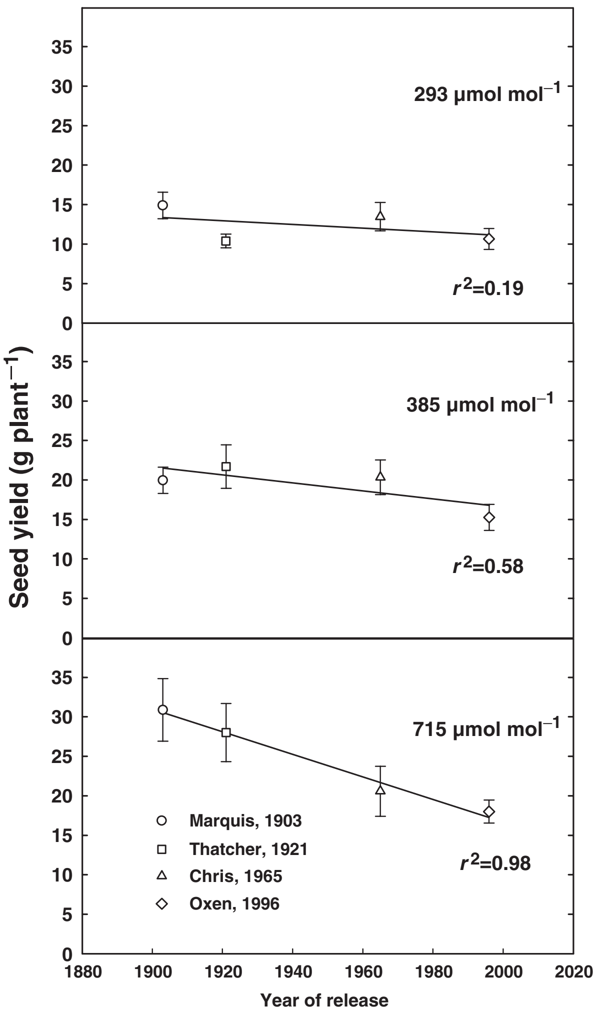

Fig. 2 Seed yield of different Spring wheat lines (Marquis, ○; Thatcher, □; Chris, △; Oxen, ◇) as a function of year of release (1903, 1921, 1965 and 1996, respectively) when grown at atmospheric [CO_2]s of 293, 385 and 715 µmol mol^{-1} These concentrations correspond roughly to the [CO_2] present in 1900, the current condition, and levels projected for the next 50–100 years. r^2 values were significant at [CO_2] values of 385 and 715 µmol mol^{-1}, indicating a downward trend for seed yield with year of release. Bars are +SE.

cultivar by [CO_2] effects were observed for both grams of flour and protein produced (Table 4). In addition to these effects, cultivars also resulted in qualitative changes in the concentration of protein within the flour, percent flour yield, break flour yield, milling score, bake water absorption, bread loaf volume and harvested ash content; increasing [CO_2] effects were significant for concentration of protein in the flour ($P = 0.08$), break flour yield and harvested ash; interactive effects were also observed for harvested ash and break flour yield ($P = 0.056$).

Discussion

Recognition of environmental limitations and selection for optimal yield performance has been crucial to the success of wheat production during the 20th century. From the current study, and others (e.g. Mandersheid & Weigel, 1997; Hakala, 1998; Rogers *et al.*, 1998; Kimball *et al.*, 2001) it is clear that rising [CO_2] is an environmental parameter that results in additional wheat productivity at the whole-plant level. Preliminary studies for a number of crop species have indicated significant variation in yield among cultivars in response to elevated [CO_2] (reviewed in Hall & Ziska, 2000). While the absolute yield response to increasing [CO_2] in wheat may be dependent on nitrogen or water availability (e.g. Kimball *et al.*, 2001), these studies *in toto* indicate that assessment and selection of the most CO_2-sensitive wheat cultivars might also result in significant yield increases in a future, elevated CO_2 environment.

Has differential sensitivity among cultivars already resulted in a significant increase in yield in response to [CO_2] increases during the 20th century? In the current experiment we selected four cultivars released from 1903 to 1996 each with distinctive breeding traits. Marquis was introduced in 1903 in southern Canada (Morison, 1960). It had yields superior to any previously issued cultivar and gained in popularity such that by the early 1920s, 90% of spring wheat on Canada's prairies consisted of Marquis (Morison, 1960). Thatcher was introduced in the early 1920s and was one of the first leaf rust-resistant varieties; Chris was introduced in the mid-1960s with earlier maturity and leaf rust resistance; Oxen was introduced in the late 1990s with early heading and resistance to leaf and stem rust. All cultivars are still grown today for breeding purposes (Bonjean & Angus, 2001). Overall, it is clear that the response of wheat to recent increases in atmospheric [CO_2] is greater for the older cultivars (i.e. those released early in the 20th century e.g. Fig. 2). This is a finding similar to that of Mandersheid & Weigel (1997) for the response of traditional and modern wheat varieties to a future, projected [CO_2] increase. However, while potential yield responses to recent [CO_2] increases are possible among wheat lines, it is difficult to quantify the impact of recent [CO_2] increases on wheat yield *in situ*. First, it is difficult to separate [CO_2] effects from technological and management advances that coincided with the rapid increase in carbon dioxide concentration since the 1940s (see Amthor, 1998 for a discussion), and separate assessments of wheat growth and yield to recent CO_2 increases independent from such advances are generally not available because of methodological difficulties in obtaining preambient [CO_2] for field plots (see Polley

Table 3 Averages and statistical P-values of the two-way analysis of variance for cultivars and CO_2 concentration on reproductive characteristics at maturity for four cultivars of Spring wheat released during the 20th century (MA, Marquis (1903); TH, Thatcher (1921); CH, Chris (1965); OX, Oxen(1996)) and grown at recent, current and future CO_2 concentrations (293, 385 and 715 $\mu mol\ mol^{-1}$)

	Averages							P-values		
Variable	293	385	715	MA	TH	CH	OX	Cv. effect	[CO_2] effect	Cv. × [CO_2]
No. of mature heads	26.2	32.0	33.8	40.8	40.1	21.4	20.5	***	**	(*)
% Tillers with heads	92.2	93.5	90.9	87.8	88.0	94.8	96.3	**	*	**
Average panicle weight (g)	0.90	1.01	1.14	0.89	0.89	1.17	1.14	***	**	(*)
Seed yield (g)	12.5	19.3	24.2	21.9	19.9	18.1	14.5	**	***	*
Average kernel weight (mg)	25.2	26.6	29.2	23.4	24.0	29.6	30.9	**	(*)	–
Average kernel size (mm)	2.18	2.28	2.43	2.10	2.17	2.43	2.47	*	(*)	–
Harvest index	0.24	0.28	0.24	0.20	0.22	0.32	0.36	***	*	–

Unless otherwise specified, values are per plant.
(*)$P<0.10$; *$P<0.05$; **$P<0.01$; ***$P<0.001$.

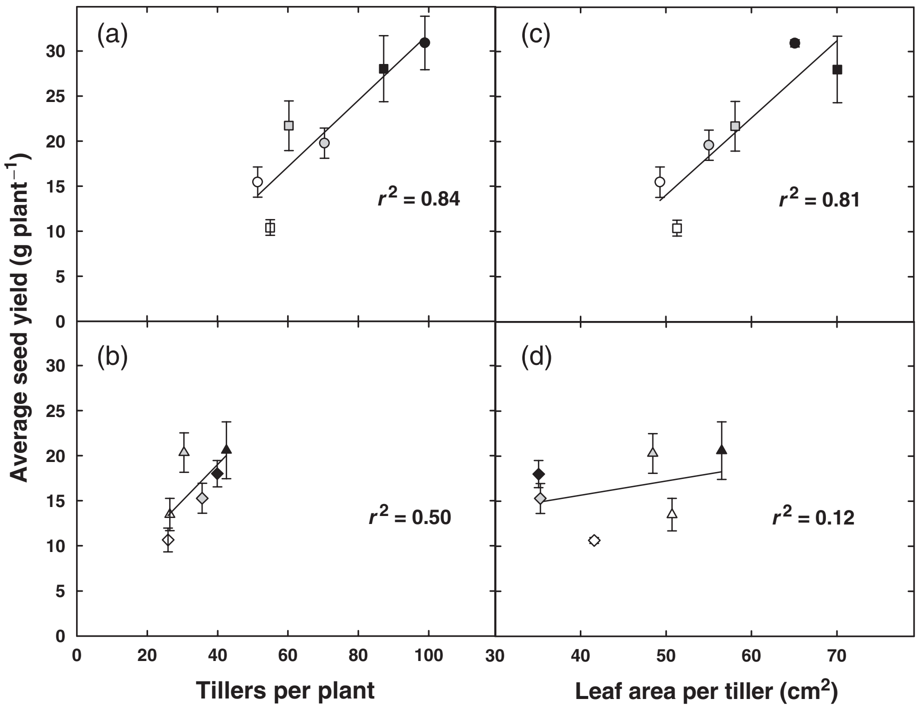

Fig. 3 Seed yield of different Spring wheat lines (Marquis, ○; Thatcher, □; Chris, △; Oxen, ◇) grown at three different CO_2 concentrations 293 (clear symbols), 385 (gray symbols) and 715 íatm (black symbols) relative to either tillers per plant (a, b), or leaf area per tiller c, d). Figures are grouped by year of release with the older (Marquis and Thatcher) and newer cultivars (Chris, Oxen) in (a, c) and (b, d); respectively. Bars are +SE. R^2 values were significant for (a–c).

et al., 1993). Secondly, as this experiment makes clear, yield characteristics and [CO_2] sensitivity at the whole-plant level have been significantly altered among wheat lines over a 100-year period as new varieties have been introduced.

Although the older varieties demonstrate a greater yield sensitivity, it is clear that breeders throughout the 20th century have selected for characteristics at the whole-plant level that have significantly contributed to potential wheat yield. For example, when averaged over all CO_2 concentrations, harvest index, the percentage of tillers with heads, average panicle weight, average kernel weight and size, all increased at the whole-plant level for Oxen (1996) relative to Marquis (1903). But if this is the case, why has not [CO_2] sensitivity increased rather than decreased with the introduction of new cultivars? Are, in fact, whole-plant characteristics associated with newer cultivars (e.g.

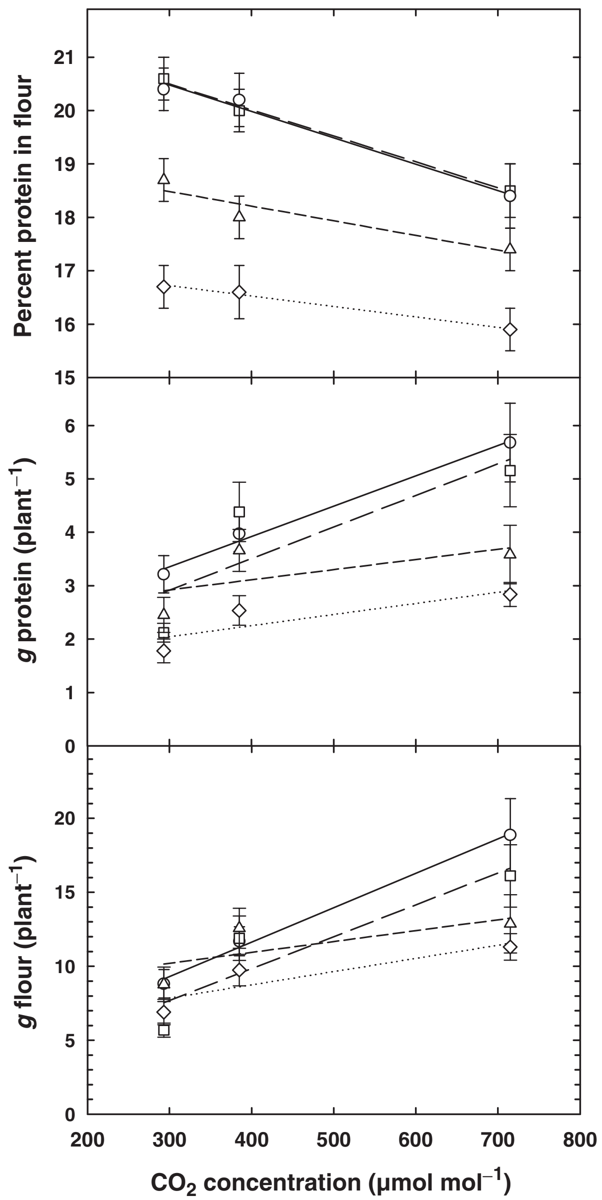

Fig. 4 Selected changes in grain quality (percent flour protein, g protein and g flour harvested) as a function of CO_2 concentration for different Spring wheat lines. Symbols are the same as Fig. 2. Statistical values are given in Table 4. Bars are $\pm$ SE.

average kernel weight) the same traits that influence CO_2 yield sensitivity? The data presented here suggest that among vegetative parameters, the ability to produce new tillers and leaf area per tiller are strongly related to CO_2 yield sensitivity above 293 μmol mol^{-1} CO_2. This is consistent with several other greenhouse and field studies demonstrating that the relative sensitivity of cereal grain yield with a doubling of CO_2 concentration was strongly correlated with an increase in tiller production, leaf area, and subsequent panicle formation (Mitchell *et al.*, 1993; Ziska, 1996; Mandersheid & Weigel, 1997; Moya, 1998). Yet, the ability to form new tillers appears to be limited among newer cultivars (Fig. 3b) (in part, perhaps, as a means to increase planting density). Overall, this suggests that empirical selection for high yield and CO_2 sensitivity are not, necessarily, contemporaneous.

But is the yield response of individual plants observed here relevant to field conditions? For example, wide spacing of single plants in growth chambers allows for older cultivars (e.g. Marquis) to have a larger grain yield relative to newer cultivars (e.g. Oxen) under ambient CO_2 concentration, a situation unlikely to occur in the field. It is important to recognize, however, that yield at the field level is a consequence both of single-plant characteristics (e.g. harvest index) and agronomic practice (e.g. spacing to maximize yield per area). While the absolute response between field and individual plants will differ, the potential yield of older cultivars to increasing [CO_2] under field conditions will be dependent on suitable agronomic practices that enhance the cultivars ability to utilize additional CO_2 as a resource for increased productivity. For example, if spacing is altered so as to allow for increased tillering, is it possible for older cultivars to match or exceed production of modern lines given the increase in atmospheric [CO_2] that has already occurred? Interestingly, field trials conducted at the Dickinson Research Extension Center at South Dakota State University in the 1980s showed no significant difference between average yield of Marquis (27.6 bushels acre^{-1}) and the average combined yield of 29 other Hard Red Spring wheats (29.1 bushels acre^{-1}) (C. Glover, wheat breeder, South Dakota State University, personal communication). Overall, while we recognize that transfer of CO_2 sensitivity from single-plant responses to field production is an ambitious task, transfer of such whole-plant characteristics (e.g. harvest index) are clearly recognized as being crucial in bolstering field productivity. Similarly, the current study suggests that selection of individual plant characteristics associated with a strong response of whole-plant yield with rising [CO_2] (e.g. tillering), could be explored and, potentially, incorporated to maximize wheat yields in a future, higher [CO_2] world.

However, in addition to recognizing quantitative changes among wheat lines, [CO_2] induced changes in quality also need to be considered. That future, projected increases in [CO_2] can reduce the concentration of wheat and flour protein, has now been demonstrated in a number of greenhouse, growth chamber and field experiments (Tester *et al.*, 1995; Blumenthal *et al.*, 1996; Kimball *et al.*, 2001) and is consistent with the current data. However, lack of change in protein concentration from 293 to

Table 4 Averages and statistical *P*-values of the two-way analysis of variance for cultivars and CO_2 concentration on wheat quality characteristics at maturity for four cultivars of Spring wheat released during the 20th century (MA, Marquis (1903); TH, Thatcher (1921); CH, Chris (1965); OX, Oxen (1996)) and grown at recent, current and future CO_2 concentrations (293, 385 and 715 $\mu mol\ mol^{-1}$)

	Averages							*P*-values		
Variable	293	385	715	MA	TH	CH	OX	Cv. effect	[CO_2] effect	Cv. × [CO_2]
Protein grain concentration (%)	20.8	21.1	19.5	22.5	21.8	19.5	18.1	**	*	–
Protein flour concentration (%)	19.2	18.8	16.8	19.6	19.3	17.7	16.4	**	(*)	–
Flour yield (%)	59.5	59.3	61.2	58.5	55.7	61.9	64.0	**	–	–
Break flour yield (%)	38.2	36.5	35.3	34.9	35.1	40.0	36.6	**	***	(*)
Milling score	59.5	56.5	63.8	56.2	51.4	63.2	68.9	**	*	–
Bake water absorption (%)	76.0	75.7	74.8	76.8	75.5	73.9	75.7	*	–	–
Bread loaf volume (cm^3)	896	1198	943	1035	1257	920	837	*	*	–
Protein harvested (g)	2.67	4.01	4.79	4.87	4.24	3.54	2.59	***	***	*
Flour harvested (g)	7.55	11.5	14.8	13.0	11.2	11.3	9.35	***	***	*
Ash harvested (g)	0.05	0.08	0.09	0.09	0.08	0.08	0.05	***	***	*

Unless otherwise specified, values are per plant. No [CO_2] or cultivar effect was observed for mixograph absorption, mixing time or bread crumb grain score.
(*)$P<0.10$; *$P<0.05$; **$P<0.01$; ***$P<0.001$.

385 $\mu mol\ mol^{-1}$ in the present experiment contrasts with the findings of Rogers *et al*. (1998) that showed significant reductions in grain protein with a [CO_2] increase from 280 to 350 $\mu mol\ mol^{-1}$. Overall, protein amounts, expressed on an individual plant basis, increased with [CO_2] and decreased with cultivar year, with a significant [CO_2] by cultivar interaction, suggesting that sufficient intraspecific variability exists for selection to maximize both grain yields and protein concentration.

In addition to changes in protein, increasing [CO_2] also significantly altered break flour yield, milling score, bread loaf volume and ash content (on an individual plant basis). Observed [CO_2] induced changes in bread and flour quality have also been observed for wheat (cv. Yecora Rojo) grown at $\sim$200 $\mu mol\ mol^{-1}$ above ambient in a FACE system, although [CO_2]-induced changes in break flour yield and milling score were not observed (Kimball *et al*., 2001). [CO_2]-induced changes in gluten composition, dough strength and mixing properties were also observed for two Australian wheat cultivars, Rosella and Hartog with recent (280–350 $\mu mol\ mol^{-1}$) and projected (350–900 $\mu mol\ mol^{-1}$) [CO_2] increases (Rogers *et al*., 1998).

Conclusions

This is the first study to quantify yield sensitivity to rising [CO_2] with respect to recent atmospheric [CO_2] for cultivars that were released over a 93-year period during the 20th century. Since these cultivars have not changed genetically, differential [CO_2] sensitivity observed at the whole-plant level is because of [CO_2]-induced morphological and/or phenological traits. However, the traits selected by breeders to increase yield during this period (e.g. kernel weight), are, surprisingly, not the same traits associated with a strong yield response to rising [CO_2]. Rather, responsiveness to increasing [CO_2] was associated with morphological attributes such as the extent of tillering: characteristics that also showed a consistent correlation with wheat yield and future, projected atmospheric [CO_2]. Recognizing that agronomic field trials are not yet available, these data, while preliminary, suggest that such individual plant traits could, potentially, be incorporated into wheat selection programs to maximize yield as atmospheric [CO_2] continues to increase. However, given the number of qualitative changes that are adversely affected by [CO_2], nutritional criteria (e.g. higher protein concentration) should also be considered.

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